

Recruitment and Food-Retrieving Behavior in *Novomessor* (Formicidae, Hymenoptera)

II. Vibration Signals*

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Summary. 1. In this article, we report the communicative effect of stridulation signals in *Novomessor cockerelli* and *N. albisetosus* during foraging.

2. The structure of the stridulatory organ and the main characteristics of airborne and substrate-borne stridulation signals are described.

3. The stridulation signals are not perceived by the ants over any appreciable distance. However, workers that contact an object transmitting stridulatory vibrations stay at this probe significantly longer than at a nonvibrating control probe.

4. An information transfer analysis was performed by comparing the probabilities of occurrence of different behavioral acts in workers both before and after contacting either a 'stridulatory' test probe or a 'silent' control probe. Stridulation did not affect the behavior of food carriers; diggers that carried debris from the nest were slightly but significantly influenced; but a remarkable change did occur in the probabilities of behavioral acts by scout ants.

5. Stridulation alone does not release a specific behavioral response but rather enhances more or less a change to different behavioral activities in workers.

6. In a series of field experiments, it was shown that a prey object too large to be retrieved by one ant stimulates the finder ant to stridulate. It was further demonstrated that the vibrational signals received by a second ant that also contacted a prey enhance the release of chemical short-range recruitment signals by this ant. In our experiments, the facilitating effect of stridulation on chemical recruitment led to a time advance of 1–2 min in both the recruitment of workers and in the retrieval of large prey objects by groups of foragers. It has been demonstrated that the rapid group retrieval of large prey objects enables *Novomessor* workers to successfully compete with mass-recruiting ant species such as *Solenopsis* and *Iridomyrmex*.

7. Significantly more digging is only released at a 'stridulatory' test probe if the probe is offered very close to a nest entrance.

* Dedicated to Prof. Dr. M. Lindauer on the occasion of his 60th birthday

8. Stridulation in ants seems to be a mechanism for modulating the state of readiness of receivers to react to other stimuli (modulatory communication). The stridulation signal adjusts the distribution of the worker force to a given situation and to group needs in a graded fashion, but does not by itself release specific behavioral reactions. This phenomenon is compared with similar functions in other communication systems of complex animal societies.

Introduction

The capacity to produce sound by stridulation is very common in ants. Markl (1973) surveyed 1354 species belonging to 205 out of 267 genera (see classification by Brown, 1973) and including 85% of all genera of those subfamilies (i.e., Ponerinae, Pseudomyrmecinae, and Myrmicinae) in which a stridulatory organ occurs. He found a well-developed sound-producing apparatus in 100% of the pseudomyrmecine, in 48% of the ponerine, and in 83% of the myrmecine species. It is therefore surprising how little is known about the biological function of the capacity for acoustical signaling in the ants, as noted in literature reviews and more recent research articles by Markl (1967, 1968, 1970, 1973), Spangler (1967a and b, 1974), Markl et al. (1977), and Zhantiev and Sulkhanov (1977).

All ant species studied up to now stridulate persistently when prevented from moving freely by whatever means. In leaf-cutting ants (*Atta*), it was found that when conditions allow transmission of stridulatory body vibrations through the substrate, workers perceive these vibrations and are attracted to them. If the source is covered by soil—for example, when workers are trapped after a nest cave-in—the nestmates attracted to the vicinity dig where vibration intensity is high and thus rescue the trapped ants. Since sexual castes, especially the huge queen, produce vibrations of highest intensities, they attract a disproportionate share of the rescuing activities (Markl, 1965, 1967). Spangler (1967a and b) recorded sound production in *Pogonomyrmex* under a variety of circumstances. Although workers did not orient or dig to a source of stridulation, excavation in the direction of buried nestmates was accelerated by vibrating the substrate with replays of previously recorded stridulation. The basic response appeared to be an increase in the activity level. During courtship behavior of harvester ants (*Pogonomyrmex*), Markl et al. (1977) found stridulation not to be involved in mate selection and actual mating behavior (i.e., reproductive isolation). However, females stridulated regularly when they were no longer willing to copulate but were still being courted by males. This signaling seems to inhibit the courting behavior in males and thereby frees the females for take off from the mating leks.

In a number of ant species (e.g., *Pogonomyrmex*—Spangler, 1967b; *Odontomachus*—Markl, unpublished observations), it has been observed that workers also stridulate when they contact water or food. However, it is well known that ants employ a variety of chemical communication signals during foraging (see Wilson, 1971; Hölldobler, 1977); furthermore, they have never been found to be able to perceive airborne stridulatory signals, and the vibrational energy

transmitted into the substrate by free-standing ants is so little (Markl, 1967, 1968) that it has seemed quite unlikely that stridulation signals play a communicative role during social foraging activities. On the other hand, we found that *Novomessor* regularly stridulates upon contact with large prey items. We therefore investigated whether these stridulatory stimuli, in addition to the chemical recruitment signals described in part I (Hölldobler et al., 1978), regulate social prey-retrieving behavior.

Material and Methods

Field observations and sound recordings were made in July 1975 in a flat open mesquite-acacia desert between Portal, Arizona, and Rodeo, New Mexico. There, *Novomessor cockerelli* usually were active during the night, beginning late in the afternoon and extending activity into the early morning, usually ending by 8–9 a.m. Most experiments were performed in the early morning in the vicinity of the nest mounds of a total of about 20 nests. A few additional experiments were performed with *N. albigesotus* at Cave Creek Ranch in the foothills of the Chiricahua Mountains.

In the field, the airborne components of stridulation were easily monitored with a Holgate Ultrasonic Receiver (Holgate of Totton, Ltd., England; sensitivity -60 dB re 1 V/ μ bar; response flat ± 2 dB between 5 and 40 kHz, ± 10 dB between 1 and 100 kHz), the BFO circuit of which allows a rough estimation of the signal's maximum intensity. The sensitivity of this receiver is high enough to pick up stridulation signals from *Novomessor* workers over a span of several centimeters. Stridulation activity could also be visually recognized with some experience from the typical gaster motions. To measure signal parameters, the airborne signals were recorded with calibrated Bruel and Kjaer condenser microphones, types 4133 (20 Hz to 40 kHz ± 2 dB) or 4145 (20 Hz to 19 kHz) on a Nagra SJS magnetic tape recorder (25 Hz to 35 kHz at 15 ips recording speed). One recording was made through the Bruel and Kjaer 4135 microphone (10 Hz to 100 kHz) using a SABA-Precision Instr. 6204 tape recorder (50 Hz to 100 kHz) (see Fig. 3). During the recording, the ants were held with a thin pair of forceps at 0.5–1 cm distance from the microphone in front of a nonreflecting background in order to avoid signal distortion. Solid-borne stridulatory vibrations were recorded through calibrated Bruel and Kjaer accelerometers (types 4335, 4338, 8306, and 8307) with 4335 (0.1–15 kHz) and 8307 (0.1–30 kHz) yielding best results.

Tape recordings were filmed from a Tektronix 5113 storage oscilloscope with a Tönnies Recordine oscilloscope camera; spectrograms and spectral sections were produced by a Sonagraph 7029 A (Kay Elemetric Corp.), at reduced tape speeds when necessary. The SEM micrographs of the stridulatory organ were taken on the AMR 1000 A Scanning Electron Microscope of the Harvard University Museum of Comparative Zoology Laboratories.

The techniques of the behavioral experiments will be described in the pertinent sections. For statistical comparisons of differences, t - and χ^2 -tests were used as indicated in the text. A difference was regarded as significant if error probability for rejection of the null hypothesis was $P \leq 0.01$.

Results

I. The Stridulatory Organ and the Characteristics of the Stridulation Signals in the Workers of Novomessor

1. The Stridulatory Organ

As in all ants possessing the stridulatory organ, that of *Novomessor* consists of a file (*pars stridens*) situated mediodorsally on the anterior end of the first gastric tergite, which during sound production is actively moved forward (up-

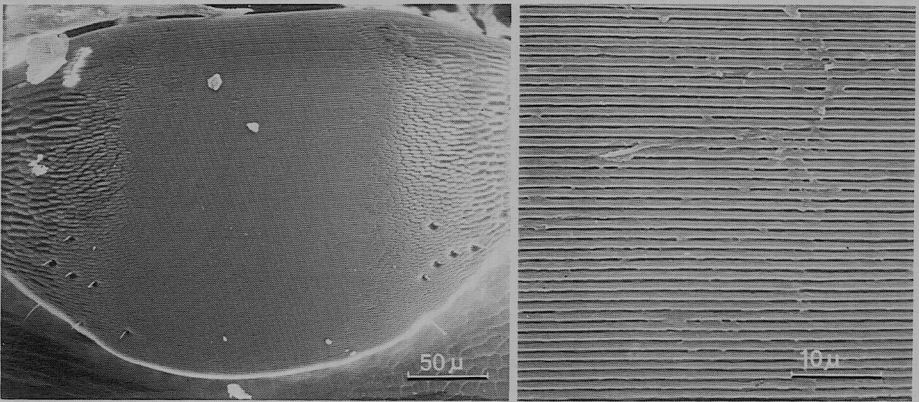


Fig. 1. Scanning electron micrographs of the stridulatory file of a *N. cockerelli* worker

Table 1. Morphologic characteristics of the stridulatory files of large *Novomessor* workers and of *N. cockerelli* queens. Averages $\pm$ standard deviations for *n* measurements

	<i>N. cockerelli</i>		<i>N. albisetosus</i>
	Worker <i>n</i> = 10	Queen <i>n</i> = 4	Worker <i>n</i> = 5
Greatest length (μm)	222 $\pm$ 24	361 $\pm$ 43	208 $\pm$ 16
Greatest breadth (μm)	139 $\pm$ 11	254 $\pm$ 23	130 $\pm$ 14
Number of ridges in file	204 $\pm$ 13	254 $\pm$ 14	211 $\pm$ 9
Distance between ridges in the center of the file (μm)	1.0 $\pm$ 0.1	1.4 $\pm$ 0.2	1.0 $\pm$ 0.2

ward) beneath the sharp posterior edge of the postpetiolar tergite (scraper, *plectrum*). During the downward motion of the gaster (backward motion of the file), the two parts of the organ are either fully disengaged—resulting in a silent interchirp interval—or only partially, which leads to secondary pulse trains of quite variable amplitude and duration between the main chirps. The neuromuscular control of the stridulatory motion seems to be the same as described for *Atta* (Markl, 1968).

Figure 1 shows SEM graphs of the stridulatory files of *N. cockerelli* and *N. albisetosus*. In Table 1, the basic morphologic characteristics are given as taken from nail-polish replicas of the files. There is no significant difference in the measurements of the files of workers of both species, whereas the female sexual of *N. cockerelli*, due to its larger body size, has a significantly larger file. No males have been studied. Typically, the ridges of the file are spaced more narrowly at the ends of the file than in its middle portion. Studies in *Atta* have shown that usually only that central part is used for signal production, which seems also to be the case in *Novomessor*.

2. Stridulation Signals

Like other kinds of ants, workers of *Novomessor* stridulate persistently when they are held at any part of their body. And as in other myrmecines that cannot sting (e.g., attines), their stridulation usually consists of long series of repetitive pulse trains (chirps), each pulse being the result of the impact of the scraper on the ridge of the file (for the physics of stridulatory sound production, see Markl, 1968). By measuring chirp and interchirp durations, interpulse durations, and numbers of pulses per chirp, the signal can be characterized quantitatively (Table 2). Figure 2 presents some typical oscillograms of the signals as recorded through air or as substrate vibrations. The 'distress signals' of ants held by forceps vary considerably. This is partly due to the struggling motions of the ants attempting to free themselves. However, even when a worker stridulates while not struggling, there still exists considerable variance of all parameters. Table 2 and Figure 2 also contain data from recordings made in the field of the stridulation produced by unimpeded workers when contacting food ('alarm') and of workers of neighboring nests when engaged in a fight. As can be seen, there is no significant difference in the parameters between the stridulation under these 'free' circumstances and the 'distress' stridulation of hand-held ants, except that in typical alarm stridulations, only relatively few chirps are produced in a series (Fig. 2 shows the longest series recorded).

The full range of variability of *Novomessor* stridulation is nevertheless still grossly underestimated by the data given in Table 2 because no recordings were included of workers trapped under soil. Even cursory inspection of such recordings shows that under these conditions variance of all parameters is greatly increased. Comparison of the signal data from the two species of *Novomessor* yields no overall statistically significant differences even though there is such difference for some measures. But for the reasons already given, these differences, as well as those that exist between *N. cockerelli* workers and females, should not be overinterpreted. From Table 2, one can also compare signal parameters recorded from *N. cockerelli* workers and females by holding them with forceps in front of a microphone or by fastening them to an accelerometer in various ways (some of them equivalent to the situation in the behavioral tests; see p. 192): again there is no clear-cut difference between the stridulatory patterns, except for a tendency for chirps to be longer and to contain more pulses in those ants that are firmly attached to a substrate.

In summary, it seems reasonable to conclude that in *Novomessor*, as in all other stridulating ants studied up to now, the signal has a variable time structure with monomodal distribution of all parameters studied. No evidence exists to support differentiation into more than one type of signal structure. In that sense, it is a nondifferentiated, unitary, elemental signal, fully characterized by a few gross ranges of duration and pulse numbers: chirps of ca. 100 (25–200) ms duration and containing 70 (10–140) pulses are interrupted by ca. 100 (70–400) ms intervals (into which shorter, less intensive, and more variable intermittent chirps can be fitted), thus yielding a typical repetition rate of main chirps around 4–5/s and pulse repetition rates within chirps of 600–1000

Table 2. Signal characteristics of distress stridulation (with a few data of stridulation during a fight or while alarming at a food source) of workers of *N. cockerelli* and *N. albisetosus* and of female sexuals of *N. cockerelli*. Averages $\pm$ standard deviations and (ranges). All time measurements in ms. A: chirps produced by upward motion of the gaster, typically of high amplitude. B: chirps produced during downward motion of the gaster, amplitudes variable from zero to equal to that of A. Air: recording of airborne signals. Substrate: recording with Bruel and Kjaer accelerometers 4335 or 8307 (as indicated in column head), to which the animals were fastened with masking tape. Vial/tape, Vial/needle: workers taped or pinned to the inside of the screw-top of a tightly sealed glass vial as explained in text (p. 192). *n* = number of measurements

	<i>Novomessor cockerelli</i> worker				<i>N. cockerelli</i> queen		<i>N. albisetosus</i> worker
	Air	Substrate			Air	Substrate	Substrate
		4335	8307 Vial/tape	8307 Vial/ needle		4335	4335
Number of animals	3	4	2	2	1	1	2
Pulse group duration	87 $\pm$ 24	114 $\pm$ 18	121 $\pm$ 16	143 $\pm$ 51	102 $\pm$ 29	89 $\pm$ 14	118 $\pm$ 21
A distress stridulation	(25–128) <i>n</i> = 50	(46–154) <i>n</i> = 50	(79–159) <i>n</i> = 30	(24–208) <i>n</i> = 30	(84–182) <i>n</i> = 20	(58–141) <i>n</i> = 20	(60–139) <i>n</i> = 20
during fight	96 $\pm$ 19 <i>n</i> = 10						
alarming at food	108 $\pm$ 22 <i>n</i> = 10						
Pulse group duration	36 $\pm$ 17	62 $\pm$ 13	62 $\pm$ 9	69 $\pm$ 30	75 $\pm$ 22	57 $\pm$ 12	83 $\pm$ 16
B distress stridulation	(16–78) <i>n</i> = 20	(21–82) <i>n</i> = 20	(41–96) <i>n</i> = 20	(11–108) <i>n</i> = 20	(8–114) <i>n</i> = 20	(28–79) <i>n</i> = 20	(49–112) <i>n</i> = 20
alarming at food	47 $\pm$ 12 <i>n</i> = 10						
Pulse group interval	148 $\pm$ 30	105 $\pm$ 21	112 $\pm$ 27	101 $\pm$ 29	124 $\pm$ 19	100 $\pm$ 13	114 $\pm$ 23
A-A distress stridulation	(123–411) <i>n</i> = 50	(84–204) <i>n</i> = 50	(81–254) <i>n</i> = 30	(74–290) <i>n</i> = 30	(96–268) <i>n</i> = 20	(88–156) <i>n</i> = 20	(72–205) <i>n</i> = 20
during fight	140 $\pm$ 23 <i>n</i> = 10						
alarming at food	129 $\pm$ 17 <i>n</i> = 10						
Pulse group interval	18 $\pm$ 7	14 $\pm$ 6	12 $\pm$ 6	15 $\pm$ 5	63 $\pm$ 24	8 $\pm$ 8	10 $\pm$ 4
A-B distress stridulation	(4–45) <i>n</i> = 20	(2–34) <i>n</i> = 20	(5–38) <i>n</i> = 20	(8–30) <i>n</i> = 20	(2–108) <i>n</i> = 20	(1–26) <i>n</i> = 20	(5–24) <i>n</i> = 20
alarming at food	13 $\pm$ 6 <i>n</i> = 10						
Pulse group repetition rate A (s ⁻¹)	4.3	4.6	4.3	4.1	4.4	5.3	4.3
distress stridulation	(0–6.8)	(0–7.7)	(0–6.3)	(0–10.2)	(0–5.6)	(0–6.8)	(0–7.6)
during fight	4.2						
alarming at food	4.2						

Table 2 (continued)

	<i>Novomessor cockerelli</i> worker				<i>N. cockerelli</i> queen		<i>N. albigipes</i> worker
	Air	Substrate			Air	Substrate	Substrate
		4335	8307 Vial/tape	8307 Vial/ needle			
Number of animals	3	4	2	2	1	1	2
Number of pulses per pulse group A	58 $\pm$ 12 (13 -84) <i>n</i> = 50	76 $\pm$ 16 (30 -102) <i>n</i> = 50	75 $\pm$ 12 (51 -105) <i>n</i> = 30	81 $\pm$ 27 (8 -138) <i>n</i> = 30	68 $\pm$ 13 (29 -94) <i>n</i> = 20	78 $\pm$ 16 (41 -120) <i>n</i> = 20	98 $\pm$ 14 (53 -126) <i>n</i> = 20
Number of pulses per pulse group B	51 $\pm$ 13 (23 -104) <i>n</i> = 20	58 $\pm$ 10 (20 -76) <i>n</i> = 20	73 $\pm$ 14 (35 -91) <i>n</i> = 20	70 $\pm$ 15 (14 -103) <i>n</i> = 20	78 $\pm$ 19 (12 -122) <i>n</i> = 20	84 $\pm$ 11 (42 -108) <i>n</i> = 20	104 $\pm$ 17 (50 -134) <i>n</i> = 20
Interpulse interval within pulse group A ^a	1.4 $\pm$ 0.4 (0.7 -4.3) <i>n</i> = 50	1.3 $\pm$ 0.6 (0.5 -5.4) <i>n</i> = 50	1.6 $\pm$ 0.7 (1.0 -4.8) <i>n</i> = 30	1.6 $\pm$ 0.8 (0.8 -5.8) <i>n</i> = 30	1.4 $\pm$ 0.3 (0.6 -2.3) <i>n</i> = 20	1.1 $\pm$ 0.5 (0.5 -2.8) <i>n</i> = 20	1.0 $\pm$ 0.3 (0.4 -2.4) <i>n</i> = 20
Interpulse interval within pulse group B ^a	0.8 $\pm$ 0.5 (0.5 -5.1) <i>n</i> = 20	0.7 $\pm$ 0.4 (0.4 -3.8) <i>n</i> = 20	0.8 $\pm$ 0.5 (0.6 -4.0) <i>n</i> = 20	0.9 $\pm$ 0.8 (0.4 -3.8) <i>n</i> = 20	0.6 $\pm$ 0.5 (0.4 -2.8) <i>n</i> = 20	0.5 $\pm$ 0.3 (0.3 -3.4) <i>n</i> = 20	0.6 $\pm$ 0.2 (0.3 -1.8) <i>n</i> = 20
Pulse repetition rate (s ⁻¹) within pulse group A	715 (230 -1400)	770 (185 -2000)	625 (210 -1000)	625 (170 -1250)	715 (435 -1700)	910 (360 -2000)	1000 (415 -2500)
Pulse repetition rate (s ⁻¹) within pulse group B	1250 (195 -2000)	1400 (265 -2500)	1250 (250 -1665)	1100 (265 -2500)	1700 (355 -2500)	2000 (295 -3300)	1700 (555 -3300)

^a All animals recorded from sometimes produce 'double pulses,' yielding a pattern of x-2x-x-2x ... pulse intervals, without recognizable correlation with the circumstances of recording. All animals can, however, also produce long chirp sequences with exclusively x-x-x- ... intervals

(200-3000) pulses/s. Depending on circumstances, especially on stimulation intensity, chirp series vary highly in their durations, from single chirps to chirping lasting a half hour.

The SPL of the airborne signals of the largest workers of *N. cockerelli*, as measured through the Bruel and Kjaer 2209 impulse sound level meter and microphone 4133, reaches a maximum of 50-55 dB (re 2×10^{-5} N/m²) at 0.5 cm distance, the larger females yielding a few more dB. Substrate-borne vibrations were measured between 0.1 and 10 kHz with the Bruel and Kjaer 4335 accelerometer, to which the ant's ventral side was firmly pressed by a strip of masking tape, leaving the gaster free to move. Although this arrangement can yield only a first estimate for the vibration intensity that the animal could transmit

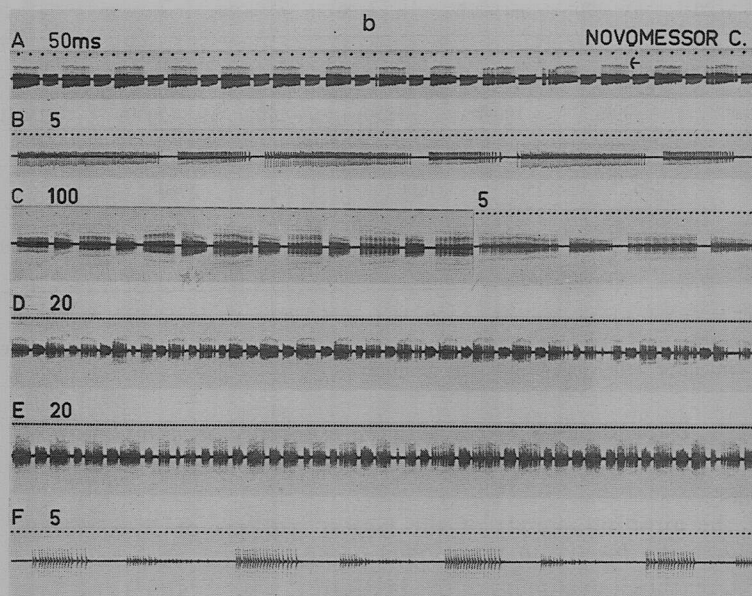
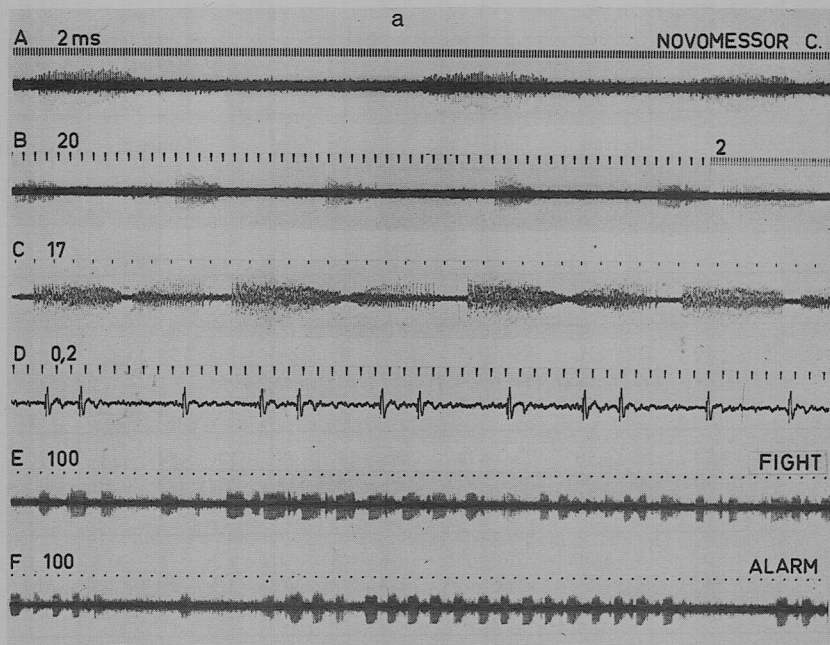


Fig. 2a and b. Oscillograms of stridulation signals from *N. cockerelli* workers recorded in air (a) or as substrate vibrations (b) with different transducers and under different conditions. Numbers refer to time-marker spacings in ms. **a** A and D: Recorded through microphone 4135 (Bruel and Kjaer); C: microphone 4145; B, E, and F: Holgate Ultrasonic Receiver; in E the recording was made during a fight between two workers from different nests; F shows stridulation of a worker ant at a newly discovered bait. **b** A and B: Recorded through accelerometer 4335; C-F: accelerometer 8307; in C the worker was fixed to the inner side of a glass vial by masking tape, in D-F by a needle through the thorax; E: continuation of D after 5 min continuous stridulation

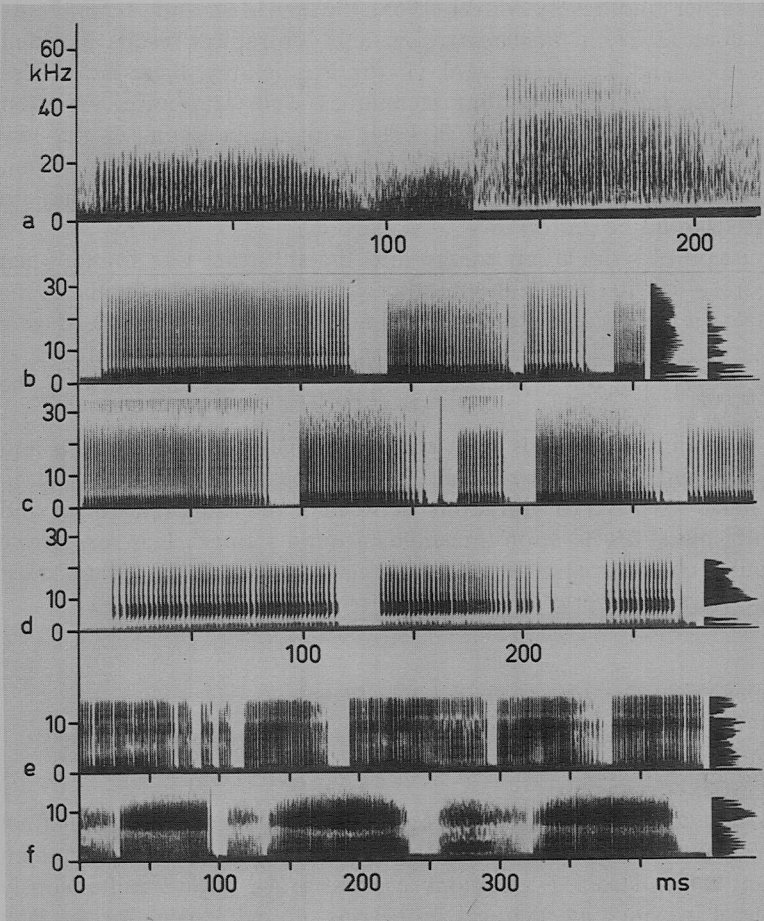


Fig. 3a-f. Spectrograms and spectral sections (right: b, d, e, and f) of stridulation signals from *N. cockerelli* (a-e) and *N. albigetosus* (f) workers recorded in air (a Bruel and Kjaer microphone 4135; right part: low cut-off filter setting 5 kHz) or as substrate vibrations (b, c, and d accelerometer 8307; e and f: accelerometer 4335). In b, e, and f the ant was taped directly to the accelerometer; in c and d the accelerometer was connected to the outside of a glass vial, to the inside of which the ant was taped

into a substrate completely surrounding it, it can be used as an approximation. Peak-to-peak values ranged 3–10 cm/s^2 , depending on the ant's body size; in female sexuals it reached 21–35 cm/s^2 . Vibration amplitudes dropped sharply with distance from a stridulator that was firmly pressed to a compact substrate; in one example—on a stone plate—from 6 cm/s^2 at the source, over 3 at 1 cm, and then to below 2 at 2 cm distance (equivalent to background noise).

Figure 3 shows the spectral energy distributions of airborne and solid-borne stridulation signals in spectrograms and spectral sections. The signal has a broad-band spectrum in both conditions. Airborne there is signal energy between 0.5 and 40 kHz, with traces beyond, as evidenced with the Holgate Receiver.

This confirms earlier findings by Markl (1965, 1968) in *Atta* and *Acromyrmex* and by Markl et al. (1977) in *Pogonomyrmex*, and contradicts results reported by Spangler (1967b) and Kermarrec et al. (1976). Presumably, these differences are caused by using different recording techniques. Substrate-borne vibration energy is distributed between 0.1 and 30 kHz, with a maximum in the low range (1–10 kHz); the exact position of the maximum depends very much on the mode of transmission from the ant's body to the transducer, so that no special emphasis should be put on it.

No transmission of stridulation energy into the substrate was found when an ant stood freely on its legs without other parts of its body touching the ground. However, if one records from material into which a worker bites during stridulation, vibrations of several cm/s^2 p-p amplitude can be monitored at close distance, depending on geometrical and physical characteristics of the material.

Vibration reception in ants has been studied by Markl (1970) in *Atta* and by Fuchs (1976a and b) in *Camponotus*. In both cases, workers have been found to be most sensitive to vibrations between a few hundred Hertz and a few kHz, with lowest acceleration thresholds around 1 cm/s^2 . It is reasonable to assume similar characteristics for *Novomessor* workers, making them most sensitive to the vibration energy in substrate-carried stridulatory signals.

II. The Communicative Function of Stridulation Signals

1. Experimental Procedure

In order to study whether stridulation signals have a communicative effect on workers of *N. cockerelli* outside their nest, it was necessary to expose them to the signal under standardized conditions at a test probe while simultaneously running a control in which an identical probe was offered, except for the lack of stridulation ('silent control'). To get effects as conspicuous as possible, the test probe should offer the signal continuously and as strongly as possible without going beyond the natural maximal signal intensity and without changing the signal pattern. These requirements were met by the following procedures.

Test Probe. Ten workers of *N. cockerelli* were placed into a screw-top glass vial 48 mm long and 14 mm $\varnothing$ and pressed to the bottom with a cotton-wool plug. The screw-top was tightly sealed with several layers of masking tape. Under these conditions, some or most of the workers kept stridulating over periods of 10 min each, producing a quasi-continuously stridulating probe. The experiment could proceed without interference from any chemical signals, since, as shown in control experiments, the latter could not penetrate the sealed screw-top. Stridulation intensity at the vial bottom against which the ants were pressed was in the same range as when it was recorded directly from the ants' bodies.

In a separate arrangement, we introduced only one worker into the vial. It proved to be especially easy to release long-term stridulation by taping the

worker by its head and thorax or by pinning it through its thorax to the inner cork layer of the screw-top. In five counts, continuous stridulation by these confined workers lasted 6–20 min (average 11.6 min) and was followed by a long time of intermittent stridulation. Food bait could be connected to the probe by fastening a water-soaked raisin to the outside of the screw-top with a strip of masking tape. Stridulation intensity at the vial-top of the probe was very similar to that recorded directly from a worker's body.

Control Probe. Control probes were initially prepared exactly as the test probes, except that the workers introduced into the vial were rendered 'mute' by crushing their petiolar ganglion. Later, we used empty control vials, since it turned out that they were not treated differently from control probes containing muted workers. Under field conditions, it was almost impossible to completely exclude any influence caused by residual chemical signals clinging to the outside of the vials even after they had been sealed. Therefore, we attempted to randomize this effect by switching control and test-probe vials after every single experiment, and by using freshly cleaned vials as often as possible.

2. Is Stridulatory Vibration Attractive to Foragers When Offered Without Bait?

In a paired array, one test probe containing ten stridulating workers, and a control probe, were placed next to an *N. cockerelli* nest. During a 5-min test period, a count of the workers in contact with these probes was made at 1-min intervals. After each 5-min period, the position of both probes was exchanged in order to control for the site-specific approach rates of foragers. In 32 tests, the average summed attendance of foragers was 8.7 ± 4.6 at the control and 12.8 ± 6.5 at the test probe (1.7 vs. 2.6 per min). The nearly 50% higher attendance is significant at $P < 0.001$ (paired *t*-test).

Is this difference caused by the fact that more ants are attracted to the test probe or that those who contact it by chance stay longer than at the control? This question was answered by counting the arrival rate at both probes during twenty 1-min test periods. The rate was 7.7 ± 2.5 workers/min at the control and 7.2 ± 3.1 at the test probe. The difference is not significant; the arrival rates are equal. The time individual ants spent at the probe from arrival to the moment they moved away by more than 1 cm was measured at both probes for 20 workers each and found to be 15.7 ± 12.8 s at the control and 28.6 ± 21.9 s at the test probe. The 82% difference is significant at $0.01 < P < 0.05$ (*t*-test). Hence, contacting workers stay longer at the test probe. Since the relation between the number of animals present at the probe (*x*), arrival rate/min (*r*) and staying time in seconds (*s*) is simply defined by $s = 60 \text{ } x/r$, one can calculate expected values of *s* for the arrival rates and numbers of workers found at test and control and compare them with empirically determined staying times. The result is:

Probe	Values of s	
	Expected	Measured
Control	13.6 s	15.7 $\pm$ 12.8 s
Test	21.3 s	28.6 $\pm$ 21.9 s

Differences between expected and determined values are not significant. This means that the simple formula describes the behavioral process adequately.

From this series of experiments, we can therefore conclude: workers of *N. cockerelli* are no more attracted over any appreciable distance to the stridulating test probe than to the silent control. However, once they have contacted a stridulating probe, they stay there 50–100% longer, even if there is no food reward. This demonstrates that they can perceive stridulation signals upon close contact with the source.

3. The Communicative Effect of Stridulation Signals at the Unrewarded Probe

How do stridulation signals affect the behavior of ants at the probe? Does the perception of the vibrations release in them the production of stridulation signals? During twenty 1-min observation periods each at control and test probes, the average number of chirp series per worker present was monitored with the Holgate Receiver and was found to be 0.03 ± 0.1 at the control and 0.19 ± 0.31 at the test probe ($P < 0.01$; *t*-test); thus, very little stridulation is released upon contact with the probes, although still significantly more so at the stridulating one.

From visual inspection, one gets the qualitative impression that contacting workers gape their mandibles more often at the test than at the control probes; it is also common to see them push their mandibles between the probe and the surrounding soil, sometimes even to lift soil particles. In order to quantify this impression and because Markl (1965, 1968) had found enhanced digging under similar conditions in *Atta*, both probes were pushed into the sandy soil at different distances from the nest opening and counts were made of the number of digging reactions (particle lifting, digging with legs, mandible boring between probe and soil) occurring per minute and per worker in contact with the probe. After 5 min, the positions of the probes were exchanged in order to control for site-specific effects. One 10-min experiment was run each at 50, 25, and 10 cm distance from the nest opening. The averages and standard deviations of digging reactions per worker per minute were:

Probe	Distance from nest (cm)		
	50	25	10
Test	0.9 $\pm$ 1.3	2.2 $\pm$ 1.5	4.1 $\pm$ 2.3
Control	0.6 $\pm$ 0.7	1.8 $\pm$ 1.3	2.3 $\pm$ 1.4

The differences between test and control were insignificant at 50 and 25 cm but significant ($P=0.05$; paired t -test) at 10 cm. In addition, it was found that at both probes significantly more digging occurred closer to the nest entrance (10 cm) than further away from it (50 cm) ($P=0.01$). Thus, both probes released some digging activity significantly. This result is comparable to the findings of Markl (1965, 1967) and of Spangler (1967b) in other myrmicine ants. The distance dependence of this effect may result from the fact that workers involved in nest construction are more likely to contact the probes close to the nest entrance. The nest-construction activity is especially prominent in *Novomessor* late in the morning shortly before patrolling on the surface of the nest comes to a rest; these experiments were performed during this time.

These initial observations encouraged us to investigate further the possible communicative function of stridulation signals. Communication is a process by which the behavior of one animal, the emitter of a signal, influences the probability of occurrence of behavior in another animal, the receiver. To learn whether stridulation has a communicative effect thus defined, we collected data that could be subjected to statistical information analysis to yield a quantitative measure of the communicative effects of the signals on the receivers (Shannon and Weaver, 1949; Quastler, 1958; Attneave, 1974; for a review, see Wilson, 1975; Steinberg, 1977; and for recent applications on particular biological communication systems, see Fuchs, 1976b; Kramer, 1976; Pruscha and Maurus, 1976).

Since the stridulation signal can be regarded as an undifferentiated elementary message unit (see p. 187), we needed only to investigate its influence on the probability of occurrence of defined behavioral acts in defined 'classes' of workers exposed to it, i.e., of workers engaged in similar behavior. The experimental approach was similar to the one already described: a test probe containing ten stridulating workers was offered at a distance of ca. 0.3-0.5 m from a control probe put at the periphery of a *N. cockerelli* nest hill by sticking the vials into the sand. Experiments were performed in the early morning when foraging had somewhat declined but was active; on the other hand, nest-construction work around the nest entrance was sufficient to allow 'diggers' to contact the probes by chance. Our procedure consisted of watching an individual worker on its fortuitous approach to a probe and recording its actions both before and following contact. The following classes of precontact activities could be recognized under the experimental conditions:

Precontact Activity Classes (x_i ; $i=1, 2, 3$)

1. Digging (D): the approaching worker carries a soil particle or some fragment of debris from the nest opening or from a digging site on the nest hill.

2. Collecting (C): the approaching worker carries a food particle to the nest opening (a sufficient number of contacts of this class was produced by feeding the ants morsels of dog food at some distance from the nest opening and the probes).

3. Scouting (S): the approaching worker runs around with empty mandibles and no obvious occupation; this is of course a miscellaneous class, including

foragers engaged in searching, diggers who have dropped their load elsewhere, workers idling on the nest surface, etc.

The following classes of postcontact activities could be distinguished by observation:

Postcontact Activity Classes (y_j ; $j=I-VII$)

- I: *Continues* previous activity;
- II: *Throws* away its load, runs off without load (not possible from S);
- III: Stays for some time with *mandibles agape*, tries to bite into probe;
- IV: Makes short fast *circling run* returning to probe;
- V: *Digs* at probe;
- VI: *Carries* newly dug-up soil *particle away*;
- VII: *Runs* fast and straight *to the nest opening* (without food).

I and II could be classified as acts of indifference, III-VII as expressions of some kind of 'interest' in the probe. The same animal occasionally produced more than one postcontact activity consecutively (e.g., III and IV), so that the number of acts counted differs by ca. 20% from the number of ants observed. Altogether, 655 pairs of precontact and postcontact activities were classified on the basis of notes on 543 contacting workers, 342 acts of 282 workers at the control, and 313 acts of 261 workers at the test probe.

The overall distribution of the different activities x_i before contact was: 99 D; 115 C; 441 S ($n=655$). Therefore, the estimates for the probabilities $P(x_i)$ of occurrence of a given precontact activity were $P(D)$: 0.151; $P(C)$: 0.176; $P(S)$: 0.673. Table 3 gives the distribution of postactivities according to preactivity classes at control and test probes. Table 4 and Figure 4 show the resulting estimates of the conditional probabilities $P(y_j/x_i)$ for the occurrence of given postcontact activities y_j after given precontact activities x_i . Statistical significance of differences between activity distributions on control or test probes was tested by a χ^2 contingency test. The results of the statistical evaluation (Table 3) can be summarized as follows:

1. The behavior of workers *carrying food* to the nest (C) was not affected by stridulation. The ants simply carry on with their job after the contact with either probe.

2. The behavior of *diggers* (D) is little influenced by the perception of the stridulation; there is only a barely significant difference from behavior after contact with the mute control, insofar as the probability of the 'interested' activities III-VII increases slightly at the stridulating test probe, whereas that of I and II, the 'indifferent' activities, decreases. These data indicate that stridulation slightly enhances a change of activities in the digging workers.

3. *Scouts* (S) the workers with no recognizable preoccupation, are the precontact activity class that is most strongly influenced by the perception of stridulation. There is a highly significant increase in activities III-VII (VI was not unequivocally recorded) at the test probe as compared with the control. This indicates that the signal is recognized and that it influences the scouts' behavior by tending to keep them more strongly occupied with a variety of activities

Table 3. Frequency of occurrence of activities y_j ($y_1=I \dots y_7=VII$) after contact with control or test probes, depending on the activities x_i ($x_1=D$: digging; $x_2=C$: collecting; $x_3=S$: scouting) before contact

x_i	$y_j \rightarrow$	I	II	III	IV	V	VI	VII	Total number of acts
D	Control	22	6	8	2	5	3	0	46
	Test	18	4	13	4	9	5	0	53
	Sum	40	10	21	6	14	8	0	99

Statistical evaluation: No significant difference between test and control. If one pools data from I and II and III-VII, there is a barely ($P=0.05$) significant difference between test and control results

C	Control	60	0	0	0	0	0	0	60
	Test	55	0	0	0	0	0	0	55
	Sum	115	0	0	0	0	0	0	115

No significant difference

S	Control	162	— ^a	19	24	26	0	5	236
	Test	94	— ^a	29	31	39	0(2?)	12	205
	Sum	256	— ^a	48	55	65	0(2?)	17	441

Highly significant difference between results at control and test probes ($P<0.001$) due to relative increase in activities which are *not* a continuation of precontact behavior after contact with the test probe

^a Not possible

Table 4. Estimates of the *conditional probabilities* $P(y_j/x_i)$ for the occurrence of postactivities y_j after preactivities x_i at control and test probes, calculated from data in Table 3

	x_i ↓	$y_j \rightarrow$	I	II	III	IV	V	VI	VII
Control	D		0.478	0.130	0.174	0.044	0.109	0.065	0
	C		1.0	0	0	0	0	0	0
	S		0.686	0	0.081	0.102	0.110	0	0.021
Test	D		0.339	0.076	0.245	0.076	0.170	0.094	0
	C		1.0	0	0	0	0	0	0
	S		0.459	0	0.141	0.151	0.190	0	0.059

at the test probe than at the control. There is, however, no evident chaneling of activities into any single behavioral alternative among the ones monitored.

Table 5 lists the estimates of the joint probabilities $P(x_i, y_j) = P(x_i) \cdot P(y_j/x_i)$ for the occurrence of the different pre-postcontact activity pairs y_j/x_i . For that, $P(x_i)$ was estimated from the pooled precontact activity distribution at test and control probes. Table 5 also gives $P(y_j)$, the estimated probabilities of

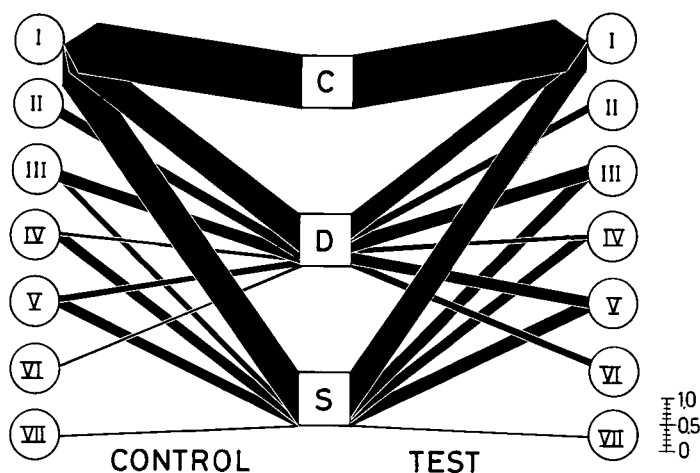


Fig. 4. Relative frequencies of behavioral transitions from precontact activities (C, D, and S) to postcontact activities (I-VII) at control and test probes (with frequencies for D, C, and S each set equal to 1)

Table 5. Estimates of the joint probabilities $P(x_i, y_j) = P(x_i) \cdot P(y_j/x_i)$ for the occurrence of the different pairs y_j, x_i of precontact and postcontact activities. $P(x_i)$ and $P(y_j)$ are also given in this table

	x_i ↓	$P(x_i)$	$y_j \rightarrow$	I	II	III	IV	V	VI	VII
Control	D	0.151		0.072	0.020	0.026	0.007	0.016	0.010	0
	C	0.176		0.176	0	0	0	0	0	0
	S	0.673		0.462	0	0.055	0.069	0.074	0	0.014
	$P(y_j)$ control			0.710	0.020	0.081	0.076	0.090	0.010	0.014
Test	D	0.151		0.051	0.011	0.037	0.011	0.026	0.014	0
	C	0.176		0.176	0	0	0	0	0	0
	S	0.673		0.309	0	0.095	0.102	0.128	0	0.040
	$P(y_j)$ test			0.536	0.011	0.132	0.113	0.154	0.014	0.040

the occurrence of the different postcontact activities after contact with test or control probe; these values are provided for the test and control probes.

From these probability estimates, calculations can be made of several measures of uncertainty in the observer about the behavior of the workers contacting a silent or a stridulating probe, with reference to the probability fields X (precontact activities) and Y (postcontact activities) and their connection. The basic formula used is the Shannon-Wiener formula for the uncertainty H of a probability distribution

$$H = -\sum P \lg P \text{ (bit)}$$

with $\lg$ = logarithm to base 2. H is also often called entropy or average information. The following relations can be derived (see Shannon and Weaver, 1949):

$H(X) = -\sum P(x_i) \lg P(x_i)$: the uncertainty about the precontact activity distribution. It is calculated to 1.24 bits (compared with maximally 1.59 bits for three activity classes according to $H(X)_{\max} = \lg 3$).

$H(Y) = -\sum P(y_j) \lg P(y_j)$: the uncertainty about the postcontact activity distributions. These have to be calculated separately for test and control probes. [$H(Y)_{\max}$ for seven classes is $\lg 7 = 2.81$ bits.] The results are:

$$H(Y)_{\text{control}} = 1.50 \text{ bits}; \quad H(Y)_{\text{test}} = 1.98 \text{ bits}.$$

These estimates show that the presence of the stridulatory signal increases the uncertainty about the postcontact activities of workers due to an increase in the diversity of postactivities and a decrease of reaction I, i.e., unchanged continuation of preactivity (exception: C).

$H(Y/x_i) = -\sum P(y_j/x_i) \lg P(y_j/x_i)$: the conditional uncertainty about the splitting into different postactivities y_j from given preactivities x_i . The results are:

Control	x_i	Test
2.13 bits	---D---	2.35 bits
0 bit	---C---	0 bit
1.47 bits	---S---	2.02 bits

The total conditional uncertainty, i.e., the uncertainty about Y that remains after the previously occurring x_i is known, is $H(Y/X) = \sum H(Y/x_i) \cdot P(x_i)$. This was found to be 1.31 bits in the control and 1.71 bits at the test probe. This means that the overall uncertainty about activities after contact with a probe is larger if the probe emitted stridulation signals, with scouts being most strongly influenced, diggers less, collectors not at all. By using these measures, the results that were previously qualitatively read from Table 2 can be precisely quantified. The statistical significances of these differences in uncertainties about events at control and test probes have already been discussed (Table 3, p. 197).

There is still a need to define a measure for the degree of relatedness between X and Y , the degree of determination of postcontact activities by precontact activities. $T(X; Y) = H(Y) - H(Y/X)$, the transmitted information, transinformation, or transmission, suits that purpose. At the control we find $T = 0.19$ bit, at the test probe $T = 0.27$ bit. This shows that, notwithstanding the higher uncertainty about the postactivities in the test situation [see $H(Y/X)$ in test/control = 1.71/1.31], the precontact activity constrains the postcontact activity more strongly when stridulation is performed. In fact, whether the stridulatory influence is strong (S), weak (D), or absent (C) depends very strongly on the precontact activity class.

The relation between these different quantities of uncertainty is explained graphically in Figure 5a. The joint uncertainty $H(X; Y)$, measuring the uncertainty of the joint system of events, is defined as $H(X; Y) = H(X) + H(Y) - T(X; Y)$. It is 2.56 bits in the control and 2.95 bits in the test situation. $H(X/Y)$, also called equivocation, is easily derived as $H(X/Y) = H(X) - T(X; Y)$; it is the conditional uncertainty about which x_i had occurred, if y_j is known to have followed. If control and test data are combined —irrespective of the presence

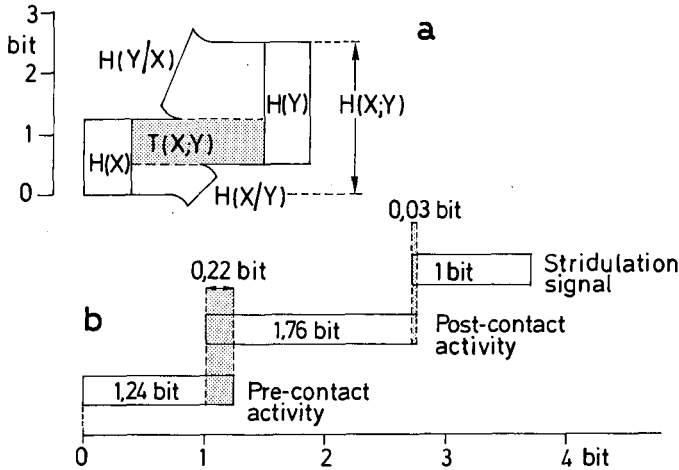


Fig. 5. **a** Schematic representation of information relations between two probability fields X and Y of interrelated events. **b** Uncertainties of precontact activity distribution, postcontact activity distribution (sum total of data from control and test probe), and of the occurrence of the stridulation signal in the test situation. The overlapping parts of the bars give the respective transinformation among the three probability fields

or absence of the stridulation signal – $H(X)$ comes out as 1.24 bits, $H(Y)$ as 1.75 bits, $H(Y/X)$ as 1.53 bits, and T as 0.22 bit.

From these results, the following conclusions can be derived: although there is a statistically significant influence of stridulation on the probability distribution of behavioral acts in workers perceiving it – proving that stridulation indeed has a communicatory effect – this influence is very small indeed. We may therefore conclude that stridulation alone, when not accompanied by additional stimuli which can release behavioral acts, only slightly influences the behavior of *Novomessor* workers outside their nests. We can say that it conveys little information among them. To use W.J. Smith's expression (1977), its message is of little meaning for the ants. However, the analytical procedure followed up to now does not allow us to determine how much information is actually transferred from the stridulation signal into the behavior of the receivers. It has to be supplemented by a more refined approach. Transinformation as calculated above measures the constraint imposed by precontact activity on postcontact activity, rather than the more interesting constraint of the presence or absence of the signal on the behavior or behavioral changes of the receiving ant. As Fuchs (1976b) has demonstrated, one can analyze information transfer from signal occurrence on the receiver's behavior if one measures the tightness of connection between the following two probability fields:

Probability Field A. The common joint probabilities $P(x_i, y_j) = P(a_k)$ of the events represented by the two-act sequences $y_j/x_i = a_k$ of precontact and postcontact activities pooled from control and test, as given in the second column of Table 6 (for example, for the sequence $y_1/x_1 = a_1 = D-I$, we have $P(x) = 0.151$; $P(y/x) = 40/99$ (see Table 3) $= 0.404$ and therefore $P(a_1) = P(x) \cdot P(y/x) = 0.061$).

Table 6. Data for the calculation of information transfer by the stridulation signal (see text for explanation).

$a_k = y_j/x_i$ = pair of precontact and postcontact activities. $P(a_k)$: common joint probabilities $P(x_i) \cdot P(y_j/x_i)$

a_k	$P(a_k)$	$H(B/a_k)$ bit	$H(B/a_k) \cdot P(a_k)$ bit	$H(B) \cdot P(a_k) - H(B/a_k) \cdot P(a_k)$ bit
D-I	0.0610	0.9788	0.0597	0.0012 (6)
D-II	0.0153	0.9384	0.0144	0.0009
D-III	0.0320	0.9780	0.0313	0.0007
D-IV	0.0092	0.9642	0.0089	0.0003
D-V	0.0213	0.9587	0.0204	0.0009
D-VI	0.0122	0.9800	0.0120	0.0002
D-VII	0	0	0	0
C-I	0.1760	1.0	0.1760	0.0002
C-II to C-VII	0	0	0	0
S-I	0.3903	0.9715	0.3792	0.0105 (1)
S-III	0.0734	0.9483	0.0713	0.0020 (5)
S-IV	0.0841	0.9731	0.0818	0.0022 (4)
S-V	0.0989	0.9477	0.0937	0.0051 (2)
S-VI	0	0	0	0
S-VII	0.0262	0.8258	0.0216	0.0046 (3)
$H(A) = 2.769$ bits			Total: 0.0288 bit = $T(A; B)$	

Probability Field B. A simpler and more easily defined concept, it describes the probabilities of occurrence ($P(b_1) = 313/655 = 0.478$) and of nonoccurrence ($P(b_2) = 342/655 = 0.522$) of stridulation in the experiments. The uncertainty $H(B)$ of field B is therefore 0.9986 bit. It is evident that system A cannot gain more information from system B than this 0.9986 bit, namely, the information on whether stridulation is present or not.

For field A , the uncertainty $H(A)$ about the two-act sequences a_k can be calculated according to $H(A) = -\sum P(a_k) \lg P(a_k)$ from Table 6. The result is 2.769 bits.

Now we can calculate $H(B/a_k) = -\sum P(b_l/a_k) \lg P(b_l/a_k)$, which is the uncertainty about whether the stridulation signal was present, which remains after the occurrence of the two-act sequences a_k is known. The procedure is as follows: the joint probability $P(x_i, y_j)$ for the occurrence of the sequence y_j/x_i in control and test can be taken from Table 5, for example, $P(D-I) = 0.072$ at control and 0.051 at test probe. The conditional probability $P(b_1/a_1)$ that $D-I$ resulted from contact with the test probe is therefore

$$\frac{0.051}{0.051 + 0.072} = 0.4146$$

and $p(b_2/a_1)$ that it resulted from contact with the control probe

$$\frac{0.072}{0.051 + 0.072} = 1 - 0.4146 = 0.5854.$$

From this, $H(B/a_1)$ comes to 0.9788 bit, as given in the third column of Table 6.

Table 7. Data for the calculation of information transfer by the stridulation signal to preactivity group S (scouts) (for explanation, see text and Table 6, with $P(x_i)$ set equal to 1)

a_k	$P(a_k)$	$H(B/a_k)$ bit	$H(B/a_k) \cdot P(a_k)$ bit	$H(B) \cdot P(a_k) - H(B/a_k) \cdot P(a_k)$ bit
S-I	0.5805	0.9717	0.5635	0.0162 (1)
S-III	0.1088	0.9467	0.1032	0.0058 (4)
S-IV	0.1247	0.9727	0.1216	0.0029 (5)
S-V	0.1474	0.9483	0.1394	0.0078 (2)
S-VII	0.0386	0.8306	0.0324	0.0062 (3)
$H(A)_S = 1.7684$ bits				Total: 0.0389 bit = $T(A; B)_S$

The conditional uncertainty about the occurrence of stridulation contributed by a given two-act sequence a_k is given by $H(B/a_k) \cdot P(a_k)$ (see fourth column of Table 6). Since the maximal uncertainty that can result from the uncertainty $H(B)$ in every two-act sequence is $H(B) \cdot P(a_k) = 0.9986 P(a_k)$ bit, the information actually gained by every two-act sequence is given by $H(B)P(a_k) - H(B/a_k) \cdot P(a_k)$ (see fifth column of Table 6).

As shown in Table 6, information gain is generally quite low in all two-act sequences, with highest values concentrated in the preactivity group S (scouts), followed by the $D-I$ sequence. In this context, information gain means the influence of stridulation on behavior, and high values for a two-act sequence demonstrate that strong behavioral shifts occurred between control and test due to the stridulation signal in the latter.

Overall transinformation $T(A; B)$ between fields B and A , i.e., the constraint exerted by the stridulation signal on the receivers' behavior, is given by $T = H(B) - H(B/A)$. It is the sum of the information gained by the different sequences a_k and comes to 0.0288 bit. Since the efficiency of information transfer can be given by $T(A; B)/H(B) \approx 0.03$, no more than 3% of the information contained in the presence of stridulation is actually transferred to the average receiving worker. The uncertainty about the subsequent behavior of a *Novomessor* worker that is exposed to conspecific contact stridulation outside the nest is therefore reduced in the observer by only $T(A; B)/H(A) \approx 0.01$, i.e., by only ca. 1%.

One can carry the analysis still one step further and ask how much information the different precontact or postcontact activity classes receive from the perception of the stridulation signal. For that purpose, the probabilities $P(a_k)$ are given by $P(y_j/x_i)$ (with $P(x_i)$ set equal to 1), which can easily be calculated from the sums of the original control and test data in Table 3. The results are given in Table 7 for the precontact activity group scouts (S) only, since collectors (C) do not gain any information (see Table 6) and diggers (D) much less (ca. 15%) than scouts. Even the scouts, however, receive only a transinformation of ca. 0.04 bit, i.e., ca. 30% more than the average contacting worker. The uncertainty about the subsequent behavior of a scout contacting a stridulation probe is only reduced by ca. 2% which, although double the value for all workers, still reflects only a marginal influence of stridulation on scout behavior.

Of the different postactivity groups, more information is going to digging (V) ($T=0.0071$ bit) than to mandible gaping (III) ($T=0.0063$ bit) and circle running (IV) ($T=0.003$ bit) while T is 0.0159 bit for continuation of the previous activity (I). This demonstrates again that the two-act sequences leading to I differ most strongly between control and test, the information measure being insensitive to the sign of the change (decrease or increase).

Summing up this section, the informational analysis allows us to draw the following conclusion about the communicative effect of stridulation signals presented to workers of *N. cockerelli* outside their nest without additional rewarding or repelling stimuli. Stridulation alone has only a very small influence on the probabilities for behavioral activities in these workers (transferred information ca. 3%). These influences can be measured and are well above significance threshold for scouts (transferred information ca. 4%), barely so for diggers, and not at all for collectors. If one compares the amount of postcontact behavior influenced by (1) the kind of precontact behavior (average transinformation 0.22 bit) and (2) the presence of stridulation (0.03 bit) (see Fig. 5b), it is quite evident that the workers' behavior under the conditions studied is only marginally determined by stridulation. Does this mean that stridulation signals are of no recognizable importance in the communication system of these ants? It would be premature to draw this conclusion without examining whether the influence of stridulation changes in dependence on circumstances in which it occurs.

4. The Effect of Stridulation Signals on Recruitment to Food Objects and on Food Retrieval:

The Communicative Function of Stridulation at the 'Rewarded' Probe

a) Methods. We have demonstrated that workers of *N. cockerelli* recruit quite efficiently to many kinds of food objects such as dead or injured insects (see Hölldobler et al., 1978, part I of this study). In order to standardize the food bait and discriminate between phases of recruitment and the retrieval of the food, the following standard object was offered either alone or in conjunction with stridulatory signals. A water-soaked raisin was fastened to the screw-top of a glass vial with a thin strip of masking tape. To the inside of the screw-top, an *N. cockerelli* worker was fastened with masking tape (or, rarely, with an insect pin stuck through the thorax) and could either stridulate freely (test probe) or was rendered mute by crushing the petiolar ganglion (control; since empty vials turned out to be equivalent, they were used at later stages of the experiments). Both test and control probes were tightly sealed by masking tape. Under these conditions, the confined workers were found to stridulate without interruption for 11.6 ± 5.1 min ($n=10$; minimum: 6 min) and with short interruptions for more than 30 min. Vibration intensity at the outer side of the screw-top was close to that of a worker directly in contact with the accelerometer. The raisin could not be carried from that probe even by a dozen workers without cutting it into pieces.

b) *The Occurrence of Stridulation upon Contact with Food.* On the basis of visual observations, supplemented by monitoring with the Holgate Receiver, it can easily be shown that *Novomessor* workers that contact a food object stridulate repeatedly as they bite into the prey and try to move it. Usually one receives a few chirps, more rarely, longer sequences (see Fig. 2). At the 'standard raisin', the number of chirp series (containing from 1 to n chirps) per minute and worker present was found to be 0.53 ± 0.59 at the silent control. This means that at a larger food object, one that easily attracts over a dozen workers who then cooperate in carrying it off, the ants produce a burst of chirping every few seconds. Does the presence of continuous stridulation enhance the production of this signal in workers contacting the food at the test probe? On the average, 0.84 ± 0.80 ($n=30$ counts) chirp series per minute and worker were counted. The difference between test and control barely misses significance. However, the difference from the frequency of occurrence of stridulation at probes without food (see p. 194: control 0.03, test 0.19) is highly significant for both control and test probes ($P < 0.01$). Thus, contact with food releases stridulation both in the absence and presence of stridulation signals, but in the latter there also appears to be some enhancing effect.

c) *The Influence of Stridulation Signals on Recruitment to Food.* In part I of this study (Hölldobler et al., 1978), we demonstrated that *Novomessor* employs a short-range and a long-range recruitment system in order to summon nestmates to large prey objects. In the following experiments, we will concentrate on several parameters of the short-range recruitment in order to see whether stridulation signals are involved in this communication system. Stridulating (test) and 'silent' (control) raisin baits were separated by ca. 30° with respect to the nest opening so that they could be easily monitored alternately by one observer sitting between the two probes. Both were laid flat on the ground at sites around which there was approximately equal worker activity. To make sure that both probes were detected soon and at about the same time, they were offered close enough to a single scout worker to be found quickly. Experiments were discontinued if wind conditions changed appreciably before their completion, if too many workers were attracted to a probe to make correct counts feasible, if no worker happened to come into contact with one or both probes, or if ants of another species (e.g., *Iridomyrmex*, *Solenopsis*, *Monomorium*) also located the food and mass-recruited nestmates to it (see part I).

Complications arose from the fact that effects turned out to depend not only on the distance of the probes from the nest (tested 1 m vs. 3 m) but also on the prevailing winds. Since we were not always able to measure the wind velocity and direction exactly, we distinguished the following cruder categories of wind condition:

1. No wind during the experiment: 'calm.'
2. Clearly recognizable wind from one direction:
 - a) Wind blowing over the probes to nest opening; i.e., signal is 'with wind.'
 - b) Wind blowing over nest opening to probes; i.e., signal is 'against wind.'

During all experiments, the largest number of *N. cockerelli* workers in the vicinity of the probes was found in the direction of the nest opening. In addition, we noted that when the wind blew, workers left the nest with a preference of ca. 1.5:1 by moving upwind (20 counts, $P < 0.001$).

In comparing the effect elicited by the stridulating probe (test) and the silent probe (control), we had to keep in mind that workers contacting food at the control probe also stridulate. Thus the major difference between the two probes was the continuous background stridulation at the test probe as opposed to no such background stridulation at the control.

The following parameters of the short range recruitment process were studied in an attempt to find out whether the continuously present stridulation at the test probe makes a difference.

1. Arrival times of finders at probes. There was large variance and no statistical difference, showing again that stridulation has no attractant effect.

2. Number of circling runs—shortly leaving the bait and looping back to it while releasing recruitment pheromone—of the finder in the first 2 min after contact with no additional recruits present. Control: 0.5 ± 0.7 ($n=10$); test: 1.0 ± 0.9 ($n=10$), no significant difference. The frequency of circling runs seems to depend only on the presence (and quality?) of food and on the inability of a single finder to retrieve it. Occasionally, similar runs have also been seen at the unrewarded probes. In these cases, however, chemical signals apparently are not released.

3. Time elapsed until first circling run of the finder occurs. Control: 25.5 ± 15.9 s ($n=10$); test: 8.9 ± 6.1 s ($n=10$). The difference is significant at $P < 0.01$ (t -test). This demonstrates a facilitating effect of continuous stridulation. Since recruits arrive at the food at a rate too high to be due to chance after a finder has contacted it, even if the finder does not circle run, one has to assume that a recruitment pheromone is also discharged by a stationary finder. Since the time lead of 17 s is much less than the time lead of recruited arrivals between test and control probes (see below), it is probable that not only does a finder recruit earlier on average at the test probe, it also does so with more efficiency (by discharging more recruiting pheromone?).

4. Time until first return run to the nest occurs (tested at 3 m distance). This can be measured at most to ca. 5 s, since only at some distance from the probe can it be discerned whether a worker is on her way to the nest. Control: 260 ± 145 s ($n=10$); test: 280 ± 170 s ($n=10$), no significant difference.

5. Time course of short-range recruitment. In Figure 6, the average numbers of workers present at control or test probes are plotted against time after arrival of the first finder at each probe. Counts were taken approximately every 10 s. In the figures, the average of three counts is averaged over the number of experiments performed and plotted for every 30 s. Differences between test and control counts were statistically analyzed using the t -test with degrees of freedom calculated according to the number of experiments (not the number of 10-s counts, which cannot be regarded as independent between subsequent counts at the same probe).

The following numbers of independent experiments were performed:

Wind conditions	Distance from nest (m)		
	1	3	Total
Calm	4	3	7
With wind	5	4	9
Against wind	4	4	8
Total	13	11	24

The reliability of individual counts was estimated to be absolute for ≤ 10 workers present at a probe, whereas counts differed by 1–3 for $10 \leq 20$ workers at a probe. We controlled well for this inaccuracy as we regarded differences to be significant only when $P \leq 0.01$ (see Fig. 6).

1. After 2.5 min, significantly more workers have been recruited to the control and test probes at 1 m than at the 3-m distance in all wind conditions.

2. At the 1-m distance, recruitment after 2.5 min at both probes is significantly higher under 'with wind' conditions than under 'against wind' and 'calm' conditions. At the same time, recruitment at the test probe is significantly higher under 'calm' conditions than under 'against wind' conditions. After 4.5 min, the same is also true for the control probe. No test is possible after 4.5 min to compare 'with wind' and 'against wind' or 'calm' conditions.

3. At the 3-m distance, recruitment is higher in test and control after 2.5 and 4.5 min under 'with wind' conditions as compared with 'against wind' or 'calm'; whereas it is only higher after 4.5 min at 'calm' as compared with 'against wind.'

The overall results of these experiments are the following. (a) The presence of a continuous stridulatory signal at the test probe enhances recruitment efficiency to a statistically significant level under all experimental condition. This effect is faster and on the average stronger the closer the food is to the nest. (b) Enhancement of recruiting is particularly strong if the wind blows over the probes to the nest opening, especially at a far distance. If no wind blows, recruitment is still stronger than when the wind blows over the nest to the probes, especially at a close distance. This agrees with our previous findings (see part I of this study), which demonstrated that short-range recruitment is mediated through the discharge of the poison-gland recruitment pheromone. Since more workers can be recruited from the direction of the nest than from the opposite direction and since workers leave the nest preferentially against the wind, the pheromone can reach the workers best if it is released upwind to the nest. The enhanced recruitment to the test probe would thus be due to earlier and more efficient release of the recruitment pheromone at the food site where stridulation signals are being continuously emitted. Thus the stridulation signals function as *communication amplifiers*. (c) This effect is clearly only temporary: after 4 to somewhat over 5 min, the difference in recruitment to both probes is gone, that is, the control draws as many recruits as the test probe.

In order to estimate the increase in efficiency of the short-range recruitment due to the activation of the finder(s) by continuous stridulation, an estimate

was made of the area between the recruitment curves in control and test situations in Figure 6. This estimate represents the worker minutes gained at the test probes as compared with the silent controls due to the time advance of 1–2 min or 3–4 min in the recruitment to the test probe:

Wind conditions	Distance from nest (m)	
	1	3
Calm	14	6
With wind	10	10
Against wind	5	4

worker minutes advance
between test and control

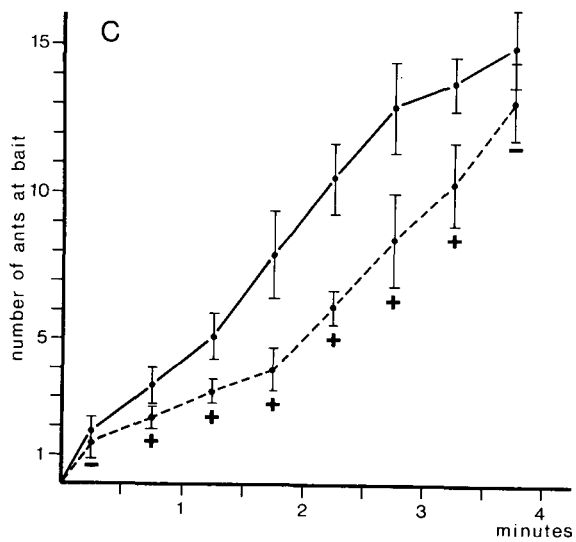
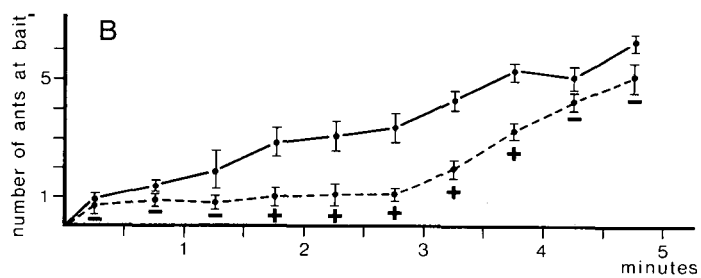
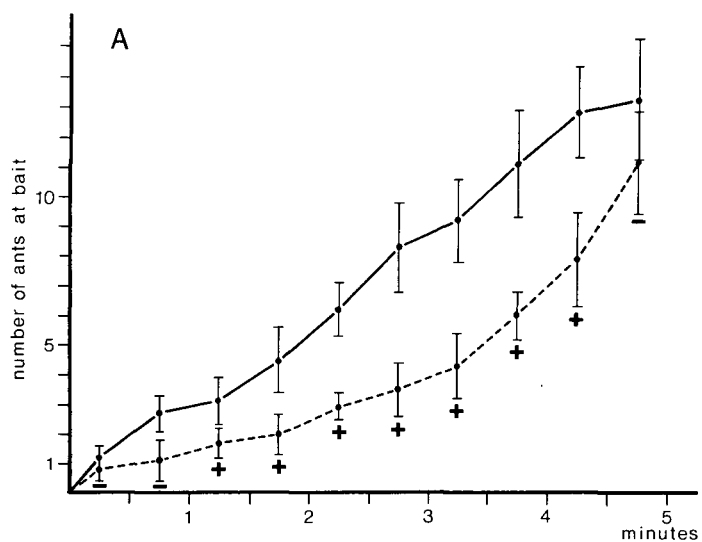
All these values are significantly different from zero

d) The Influence of Stridulation Signals on Food Retrieval. In the series of experiments to be described next, we sought to learn whether the enhancement of short-range recruitment brought about by stridulation at an object too large to be carried away by a single worker will eventually lead to faster retrieval due to the earlier assembly of a larger worker force.

For this purpose, large wet raisins were pressed onto the screw-tops of control and test probes, so that they could be torn off and carried away only by several workers. The probes were offered as previously described at 2–4 m distances from a nest opening in the 'with wind' position. A record was made of the time required for the workers to carry the raisin for a distance of 10 cm after discovery of the bait. The number of carriers involved was also counted. The averages were 199 ± 108 s with 5.1 ± 1.7 (3–8) carriers at the control ($n=10$) and 155 ± 89 s with 5.4 ± 1.6 (3–9) carriers at the test probe ($n=10$). Although no significant difference in numbers of carriers was found, the time difference is significant at $P < 0.05$. Since the time taken to carry the load over 10 cm was approximately the same (ca. 10 s) whether the ants started from the test or control probes, the time advance of ca. 45 s at the test probe is due to the fact that the necessary number of workers to tear off the raisin was reached 45 s earlier. This fits the previous data on recruitment to fixed food. It demonstrates that the faster recruitment to a stridulating object does indeed lead to faster food retrieval.

5. Experiments with *N. albigetosus*

In several pilot experiments, we attempted to learn whether the effects of stridulation are quantitatively similar in workers of *N. albigetosus* and *N. cockerelli*. Although the number of experiments was too small to warrant extensive discussion, it was our general impression that they yield results not grossly different from those just reported for *N. cockerelli*.



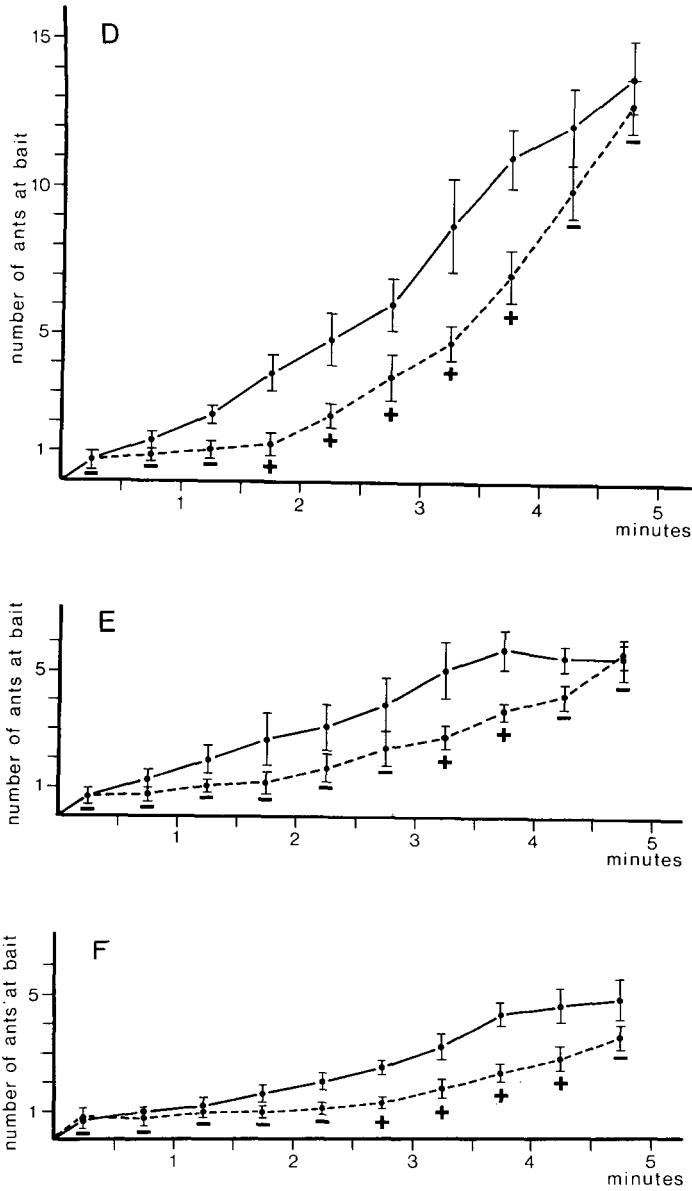


Fig. 6A-F. Average number of workers of *N. cockerelli* that are in contact with control (----) or test (—) probes after time of arrival of the first finder of each probe. Averages and standard deviations calculated from the number of replications of the experiments as given in text (p. 206). + = difference between test and control significant at $P \leq 0.01$; — = no significant difference. Wind conditions: A and B: calm; C and D: with wind; E and F: against wind. Distance between probes and nest opening: A, C, and E: 1 m; B, D, and F: 3 m

Discussion

1. The Effects of the Stridulation Signal

The results of this study can be briefly summarized as follows. Workers of *N. cockerelli* and *N. albisetosus* stridulate when they find a piece of food that they cannot handle alone. The stridulation signal is highly variable, but it constitutes an elementary and unitary signal, that is, one conveying only one type of message. It can be perceived by other workers only through the substrate at short range or by direct contact. Although the signal does not attract workers over any considerable distance, it nevertheless is effective as an arrestant and as a modulator of probabilities for behavioral changes in the receiver, as was shown by the information analysis of behavioral transitions in workers after contact with either a silent control or a stridulating test probe. These effects were studied with probes that did not offer additional releasing stimuli ('unrewarded' probes without food), so that the effect of stridulation could be investigated without the additional influence of the chemical recruitment signals released by workers finding a large food object. Analysis of communication by means of statistical information theory has the advantage of yielding results in standardized units (bits), thus making it possible to compare the communicative effects in different signal systems. Since it was the intention of this study to learn what the effect of stridulation is in the behavior of the workers outside the nest, especially during foraging, experiments were set up close enough to the nest to have sufficient worker attendance, but far enough away to exclude most of the nest workers. This is probably the reason why very little digging activity was observed at the site of the stridulating probe, since appreciable effects on digging are usually limited to the immediate vicinity of the nest opening. Markl (1967, 1973) showed, on the basis of experiments in the immediate vicinity of nest openings of *Atta*, that stridulation is a specialized underground alarm of these ants when they are trapped in subterranean nests, and it releases rescue digging in nestmates. Our studies on *Novomessor* demonstrate that the result cannot be generalized for all ants under all behavioral conditions. It works only in *Novomessor* workers that are occupied with digging in the first place. Their digging activities are, however, significantly stimulated by stridulation. Stridulation therefore acts as an amplifier for the behavior-releasing effects of other stimuli in ants ready to react to those stimuli!

2. Statistical Information Analysis

The analysis of information transfer from stridulation signals followed the study by Fuchs (1976b) on drumming communication in *Camponotus* in its general design in order to learn whether these two communication systems can be regarded as analogous. Comparison of probability distributions of easily discernible activities before and after contact of workers with test or control probes yields a small amount of transmitted information in both test (0.27 bit) and control (0.19 bit), which is, however, significantly different from each other.

In addition, it was remarkable that workers who carried food to the nest when they contacted the probes were not at all influenced by stridulation signals, whereas diggers showed a slight behavioral influence (uncertainties 2.13 vs. 2.35 bits in control vs. test) and scouts a stronger influence (uncertainties 1.47 vs. 2.02 bits).

However, not too much emphasis should be put on the absolute values of the uncertainties about the precontact and postcontact activities; only the differences between values gained at control and at test probes deserve recognition. The reason is that the different classes of precontact and postcontact activities distinguished here are by no means exhaustive classifications of the different possible behavioral states of these animals; they are only practical tools of description and classification of observations. Absolute values of $H(X)$ and $H(Y)$ evidently must change considerably with the numbers of behavioral classes defined. To allow comparisons of effects at control and test probes, it is only important that the classifications at both probes are absolutely consistent.

It has also to be admitted that the selected classification has other methodological drawbacks. While food carriers (C) and diggers (D) are quite precisely definable homogeneous classes, the scout class (S) is almost certainly highly heterogeneous, ranging from alarmed workers aiming for a food site through true scouts searching for unknown food to workers idling around the nest entrance who might function as sentinels but are not scouting for food. The same considerations apply to some classes of postcontact activities. There one might obviously object to classifying all continuation of previous activities into one class instead of making three classes out of it according to the three precontact activities. The reasons for not doing so were, first, to avoid increasing the number of postcontact classes beyond the minimum necessary (in order to make statistical evaluation of transition matrices feasible with the numbers of observations collected) and, second, to define postclasses to which access of all preclasses was theoretically possible (this failed only for transition S-II, but II could clearly not be merged with any other postclass). Another point of concern arises from the fact that in roughly 20% of the cases more than one transition was recorded for the same contacting worker (however, with no significant difference between test and control). These and other problems of informational analysis of behavioral sequences have been discussed by others (see, for example, Altmann, 1965; Slater, 1973; Wilson, 1975; Fuchs, 1976b; Kramer, 1976; Hazlett, 1977). In the case of our study, however, only the difference between uncertainty in test and control is relevant. Consequently, most of the objections raised do not apply in the present connection. For the conditional uncertainty about the postactivity which remains after the preactivity is known $H(Y/X)$, the difference calculated for all workers is 0.4 bit and ranges for different preactivity classes from 0 bit (C) over 0.22 bit (D) to 0.45 bit (S). The range of these values is comparable to that recorded by Fuchs in his study on the influence of drumming signals of *Camponotus* workers on activity distributions within their nest. Since *Camponotus* is the only ant for which similar information analysis of an 'acoustical' communication system had previously been undertaken (Markl and Fuchs, 1972; Fuchs, 1976a and

b), we employed the same procedure on the *Novomessor* data in order to measure the proportion actually communicated of the information contained in the presence or absence of the stridulation signal. This proportion was found to be 0.03 for all contacting workers and 0.04 for the scouts. Fuchs reported an overall proportion of 0.12 and 0.62 for the most sensitive preactivity class in *Camponotus*. In this case, however, only workers exposed to the signal inside the nest were studied. Into Fuchs' (1976b) Table 9, we can therefore enter with reference to *N. cockerelli* workers outside their nest the uncertainties of the behavioral acts investigated [$H(X)$ in Fuchs' notation] and the transinformation T for all workers as 2.77 and 0.3 bits, respectively, and for the scouts most strongly influenced, 1.77 and 0.04 bits. From the same table, it can be seen that low as these transinformation values are, they are not without precedent. Most significantly, Mayer (1971) — although following a somewhat different approach by applying bidirectional communication theory (Marko, 1966; Neuburger, 1970) to communication in a group of squirrel monkeys (*Saimiri sciureus*) — measured a transinformation of 0.03 bit per communicative interaction for the communication flow from dominant to subdominant male (compared with 0.21 in the opposite direction), while transinformation values up to several bits are reached in other animal communication systems (e.g., in dance communication of honeybees, Haldane and Spurway, 1954; or alarm trail communication of fire ants, Wilson, 1962). Relatively high values are also typical for communicative interaction in nonsocial arthropods (e.g., Hazlett and Bossert, 1965; Dingle, 1972; Hazlett and Estabrook, 1974; Steinberg and Conant, 1974).

3. What is Efficient Communication? 'Low- T ' and 'High- T ' Systems, Modulatory and Deterministic Communication

What conclusions can be drawn from such comparisons? Is it possible that *Novomessor* stridulation and squirrel monkey communication are especially ineffective, unimportant, poorly developed communication systems, while crabs or grasshoppers use a much more highly efficient way of communicating? This view of communication might be too simplified and prejudiced, based on the assumption that the purpose of a 'good' communication system is to exert strong control on the receiver; in other words, the more deterministic the process the better the communication. This criterion is of course the one which for very good reasons is employed by a communication engineer with respect to technical devices of human communication, and is the one routinely expressed in the standard texts of that field (see from Shannon and Weaver, 1949, to Steinbuch, 1977). It is further reflected by designations such as 'ambiguity,' 'irrelevance,' or 'misinformation' for $H(Y/X)$ and 'equivocation' or 'information loss' for $H(X/Y)$. The standard approach, however, might not be the correct way to look at animal communication systems, because it neglects entirely the fact that different environmentally defined contingencies may need differently adjusted communication systems. Where an alarm signal that warns another animal of deadly danger from an approaching predator is optimal if it strictly determines the receiver's behavior, e.g., escape, there are other circumstances

when communication plays a different and more subtle role. For example, in a monkey group with a stabilized role distribution ('rank order'), very subtle influences of communication between group members suffice to optimally adjust the behavior of groupmates toward one another. In such a case, we would expect to find quite low transinformation values for communicative interactions which leave to the group members a large degree of freedom to tune their behavior according to many other simultaneous necessities in addition to group interaction. In this view, low-'efficiency' ('low-T') communication systems serve different but no less important purposes than more highly deterministic ('high-T') systems. They gradually and smoothly influence the behavior of receivers, not forcing them into determined behavioral channels, but slightly shifting the probability for the performance of other behavioral acts. We therefore should expect such low-T systems to be most frequent in the most complex animal societies, where a large number of members perform many different tasks at the same time and where an economically efficient organization of behavior requires that the work force distribute its energy investments between the different tasks by an optimum pattern of division of labor. It would clearly be ruinous constantly to apply high-T signals whenever a shift in behavioral investment is to be elicited. Such binary responses would result in most or all of the colony doing the same thing, a pattern that may be optimal only if the colony is in imminent danger. We might therefore tentatively conclude that stridulation in *Novomessor* and other ants is such a low-efficiency communication system especially designed to produce only slight shifts in the behavioral propensities of the receiving workers. This, of course, could also provide an adaptive explanation for the fact that communication by stridulatory vibration through contact with the emitter or through the substrate is so restricted spatially, not reaching beyond the immediate vicinity of the signal source. The small number of workers influenced are either enough to perform the task, or if this turns out not to be the case, they are able to switch to more efficient, far-reaching forms of communication, exemplified in *Novomessor* by chemical recruitment.

This view of the function of stridulatory vibration also entirely agrees with what Fuchs (1976b) described as the function of drumming alarm in *Camponotus*.

If this concept is correct, we would expect that whatever behavioral change is facilitated by stridulation signals, the direction and distribution of these changes should be not so much controlled by the stridulation signal itself as by additional stimuli, adjusting the activation to the given situation. Hence, stridulation does not modify the production of specific behaviors but only the readiness to react to other stimuli impinging on the receiver at the same time, or—as we may say—its state of attention. Stridulation signals would then not be 'releasers' in the Lorenzian sense but rather a controlling device modifying the threshold for the releasing effectiveness of other stimuli, thus amplifying (or attenuating) the behavioral response to them or allowing them to pass the threshold more (or less) quickly. We propose to call a communication system of this kind *modulatory communication*; in it, signals do not release specific behavior but rather modulate the probability of reaction to other stimuli by influencing the 'motivational state' of a receiver.

If stridulation in some ants and drumming in others is truly modulatory, we would expect that its effects should be quite diverse and nonspecific, enhancing different behavioral reactions under various external conditions and in different receivers depending on their motivational states. The present study in *Novomessor*, earlier studies on the function of stridulation in *Atta* (Markl, 1965, 1967) and *Pogonomyrmex* (Spangler, 1967b; Markl et al., 1977), as well as Fuchs' (1976a and b; Markl and Fuchs, 1972) study on drumming communication in *Camponotus* fit excellently into that interpretation. To restrict the discussion to ant stridulation, it can be seen that the same kind of signal can—serve as an underground distress alarm, enhancing rescue digging in workers already inclined to digging work if there are additional stimuli releasing digging (e.g., disturbance on or in the nest);—serve as 'courtship punctuation' signal during courtship in *Pogonomyrmex*, in which females may influence males to stop pursuing them;—serve in facilitating chemical recruitment in *Novomessor* workers as shown in the present study, by stimulating a worker coming into contact with the 'stridulating' food object to immediately release chemical attractants for other workers.

Thus, recruitment is speeded up at an object when other ants biting into it are already stridulating. As our data show, not very much time is actually gained in the process: approx. 1–2 min, leading to an advance of 5–14 worker minutes at the test probe; this causes a somewhat faster food retrieval through cooperative carrying. Although the effects are statistically significant, one can ask whether such a small effect is actually of any adaptive significance for *Novomessor*. We do not have the data to finally answer that question. However, as demonstrated in part I of this study (Hölldobler et al., 1978), *Novomessor* can easily be displaced by other ant species that find the food and mass recruit to it. On the other hand, *Novomessor* is one of the few ant species in its desert biotope that employs cooperative labor to transport food items too large to be carried by a single worker. Through this adaptation, combined with the highly efficient short-range and long-range recruitment systems, which are enhanced further by stridulation, *Novomessor* can successfully hold on to many food objects that would otherwise be lost to mass-recruiting ant species. In such a highly specialized strategy, stridulation seems to fulfill exactly the function of a modulatory communication signal as conceived here: it facilitates the appropriate action in recruited nestmates with respect to the particular qualities of a food object.

This list of functions of stridulation in ants may be by no means exhaustive. For instance, we know next to nothing about the possible modulatory functions of stridulation within the nest, where frequent close body contact between workers and other castes gives optimal conditions for short-range signal transmission. In their analysis of the remarkably stridulation-analogous drumming communication of carpenter ants, Markl and Fuchs (1972) and Fuchs (1976a and b) detected quite different influences of signals on the behavior of workers inside and outside the nest. For example, the function of 'removal-enhancer' when nesting conditions turn unfavorable might easily be served by stridulation in other ant species. It would also by no means invalidate the concept derived here from experimentation outside the nest if circumstances were found when

stridulation is used with much higher 'effectiveness' in ants, that is, when stridulation is more deterministic.

The need for modulatory communication is not restricted to ant societies. It will be profitable to search for it in many or all of the more complex social systems where it could provide smoothly graded adjustments of group behavior (see Hinde and Stevenson-Hinde, 1976). It is also clear, needing no elaboration, that many linguistic, paralinguistic, and other symbolic forms of human communication serve a comparable modulating function without directly releasing or determining behavior. What may make the case of ant stridulation somewhat special is that in these insects we have a special signal-producing structure, the stridulatory organ, which appears to function exclusively as a mechanism of modulatory communication. Thus stridulation illustrates more graphically than usual a function that may in fact be deeply embedded in many or all social communication systems.

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Note Added in Proof

The statement that the stridulation organ in all ants is situated *dorsally* on the first gastric tergite is no longer true. R.W. Taylor (*Science* **201**, 979–985 (1978)) found in *Nothomyrmecia macrops* the stridulatory organ *ventrally* between abdominal sternites III and IV.